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Hunting, Age Structure, and Horn Size Distribution in Bighorn Sheep

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ABSTRACT Trophy hunting, that is the selective removal of animal for human recreation, can contribute to conservation when appropriately managed. Yet, little is known about how harvest rates or different definitions of trophy affect age structure and trophy size in harvested animals and in survivors because no controlled studies exist. To investigate the impacts of different management regimes, we developed an individual-based model for bighorn sheep (*Ovis canadensis*), based on empirical data on survival from a protected population and data on horn growth from 2 populations which differed in their growth rates. One population showed slow horn growth and the other population fast horn growth. We subjected these model populations to varying harvest rates and 2 different hunting regulations: 4/5 curl and full-curl definitions of a trophy male. We found that the effect of hunting regulations depends on horn growth rate. In

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populations with fast horn growth, the effects of trophy hunting on male age structure and horn size were greater and the effect of a change in the definition of legal male smaller than in populations with slow growth rates. High harvest rates led to a younger age structure and smaller horn size. Both effects were weakened by a more restrictive definition of trophy male. As harvest rates increased past 40% of legal males, the number of males harvested increased only marginally because an increasing proportion of the harvested males included those that had just become legal. Although our simulation focused on bighorn sheep, the link between horn growth rate and harvest effects may be applicable for any size-selective harvest regime.

KEY WORDS agent-based model, bighorn sheep, harvest management, horn growth, National Bison Range, *Ovis canadensis*, Ram Mountain, Sheep River, trophy hunting.

Trophy hunting is the killing of selected animals for human recreation. It is a widespread management practice for many ungulates, leading to the selective removal of males with large horns or antlers (Monteith et al. 2013). When properly managed, trophy hunting can be sustainable and provide a strong incentive for conservation (Leader-Williams et al. 2001). A high rate of selective removal of males with large horns or antlers, however, may lead to selection for smaller horns and reduce the availability of large trophies, as suggested for bighorn sheep (*Ovis canadensis*; Coltman et al. 2003, Traill et al. 2014, Pigeon et al. 2016). Empirical data to quantify the impact of harvest regulations on age structure and horn size of harvested males and of the overall population are scarce (Table 1) and usually rely on samples of harvested males, which can differ from the overall population (Pelletier et al. 2012, Festa-Bianchet et al. 2015). Most of these studies measured age and horn size of harvested males but had little or no information on the distribution of these traits in the population. Therefore, a modeling approach is needed to fill this gap.

We developed an individual-based model that allowed us to vary the definition of legal male and the harvest rate, 2 main tools used by managers to regulate trophy hunting of mountain

sheep (*Ovis* spp.) in North America (Wild Sheep Foundation Professional Biologists 2008). Wild sheep exhibit strong sexual size-dimorphism and males bear large curved horns that are highly sought after by trophy hunters. Definitions of legal male in North American jurisdictions are usually based on a minimum degree of horn curl, which is related to horn length and shape (Festa-Bianchet et al. 2014). Consequently, the age at which males attain legal status is mostly a function of age-specific horn growth rate. Despite strong variation in horn growth rates (Jorgenson et al. 1998), no comparative or modeling study has investigated how the impact of hunting regulations varies with horn growth rate. We took advantage of detailed empirical data from 2 populations of bighorn sheep with markedly different rates of age-specific horn growth (Jorgenson et al. 1998) and modeled hunting effects on age structure and horn length of harvested and living males. We purposely modeled 2 populations with horn growth rates near the opposite extremes of the variability found within the species. We expected that a more restrictive definition of legal ram would increase the age and horn size of harvested males but decrease the harvest. We also expected that an increasing harvest rate would lead to a younger age structure of surviving males and a shorter life expectancy for legal males. These expectations are qualitatively obvious; however, their magnitude is unknown. Our primary goal was to assess how changes in hunting regulations affect the age and horn length of harvested males and the proportion of a cohort that would be harvested rather than dying of natural causes after reaching the minimum age at which horns could attain legal size. For example, although it seems inevitable that higher harvests will shorten male life expectancy, the extent of this effect given different horn growth rates and definitions of legal ram is unknown, yet it is important to inform management decisions.

STUDY AREA

To parameterize our model, we used data on males from 3 populations: 1 unhunted population in the National Bison Range (NBR), Montana, USA, and 2 hunted populations in Alberta, Canada:

Ram Mountain and Sheep River. Hunting regulations specified a minimum legal horn size (Fig. S1, available online in Supporting Information) and an unlimited number of permits were available for Alberta residents (Coltman et al. 2003, Pelletier et al. 2012, Festa-Bianchet et al. 2014). The NBR is an 80-km^2 National Wildlife Refuge located in northwestern Montana (47° N, 114° W). The terrain is Rocky Mountain foothill (800–1,500 m elevation) supporting vegetation composed of Palouse grasslands, patches of coniferous forest, and stringers of riparian shrub and woodland. The climate is seasonal with mild winters and warm summers subject to periodic drought (Köppen classification: humid continental; Köppen 1884). The bighorn study population was established by transplant from Banff National Park in 1922. Supplemental transplants occurred during 1985–1994. Detailed individual-based monitoring began in 1979 and has been continuous since with the exception of 1987. Resident predators of bighorn include cougars (*Puma concolor*), coyotes (*Canis latrans*), golden eagles (*Aquila chrysaetos*), and American black bears (*Ursus americanus*). Wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) are transients on the refuge. Hunting and domestic grazing are not permitted and public access to bighorn range is strictly regulated.

Ram Mountain, Alberta (52°N, 115°W) is an isolated mountain complex with about 38 km^2 of alpine and subalpine habitat at 1,600–2,200 m elevation used by bighorn sheep. The climate is continental with cold winters and short summers (Douhard et al. 2017). Large predators include wolves, black bears, and cougars (Festa-Bianchet et al. 2006).

Sheep River, Alberta (50°N, 114°W) includes low-elevation (1,300–1,600 m) grasslands and high-elevation (1,800–2,600 m) alpine habitats, used by a metapopulation of bighorn sheep. The climate is similar to Ram Mountain but with more frequent warm Chinook winds in winter. The combination of lower elevation and milder climate leads to an earlier spring green-up, and the availability of an elevational gradient allows bighorn sheep to feed on nutritious growing vegetation over a long period (Festa-Bianchet 1988). Predators are the same as at Ram Mountain

(Bourbeau-Lemieux et al. 2011). Both study areas are on public land, with seasonal cattle grazing at lower elevations in summer.

METHODS

Species and Data

Our model assumes no evolutionary changes from selective harvest (Pigeon et al. 2016) and therefore provides a useful comparison for time series of horn measurements in actual harvested populations of bighorn sheep. Furthermore, we did not model density dependence in either recruitment or horn growth, despite evidence to the contrary (Jorgenson et al. 1998), because we wanted to focus on how changes in harvest strategies affect the horn size and availability of trophy males in a stable population, such as what may be expected over a time frame of decades. Because we focused on a stable population, we assumed a near-constant yearly input of 4-year-old sheep, with a minor amount of stochastic variation in recruitment.

To obtain age-specific survival rates unbiased by harvest, we used data from the NBR (Table S1, available online in Supporting Information) where sport harvest is not permitted and poaching is rare. To obtain age-specific horn growth rates, we used data from Ram Mountain and Sheep River. The data from Ram Mountain are representative of slow horn growth, which means the typical age-specific annual increase in horn length of a male from the Ram Mountain population is small. In contrast, the data from Sheep River population are representative of fast horn growth, which means the typical age-specific annual increase in horn length of a male from the Sheep River population is large (Tables S2–S3). For example, the world record ram that has the largest horns ever measured stems from the Sheep River population (Platt 2015).

A combination of density-dependent and selective effects at Ram Mountain reduced horn growth rates (Jorgenson et al. 1998, Coltman et al. 2003, Festa-Bianchet et al. 2004, Pigeon et al. 2016) so that after 1993 most males died before their horns fulfilled the 4/5 curl regulation. Consequently, we used only records from 1975 to 1992. Horn measurements could be taken only

from males that survived the hunt, such that data of individuals >4 years old (the min. age at which they can attain legal status) were biased towards males with smaller horns (Pelletier et al. 2012). This bias should be lower in the Sheep River dataset because this population is partly protected.

Survival Analysis and Horn Growth

To estimate age-specific survival rates unbiased by harvest, we used data collected during 1979–2015 from bighorn sheep in the NBR. All males in the population during this period were individually recognizable using photographically documented variation in horn and pelage characters and ear tags or notches applied at birth. We determined survival (0,1) to each age step by a capture-mark-recapture procedure in which individual identities were recorded in daily census of the population over a 4–6-week period during fall rut and defined 25 October as the first day of each male-year. We considered males seen anytime on or after 25 October during fall census as surviving the preceding age interval, whereas we considered males alive at the start of the previous age interval but last observed before 25 October as dying during the preceding interval. The rut was selected for this purpose because males are conspicuously associated with females at this time and all surviving males could be expected to participate. Conveniently, late October also corresponds to the end of the bighorn hunting season in many jurisdictions. The pool of at-risk males in each year divided into 1 of 2 re-sighting categories: those not recorded at all after 25 October and those seen on a majority of the approximately 28–42 census days. The probability of multiple re-sightings conditional on an initial sighting after 25 October was therefore 1.0. Some males in the former not-recorded category may have been undetected emigrants rather than mortalities. However, males missing in 1 year never reappeared in a subsequent year and the NBR is geographically isolated (Hogg et al. 2006).

We applied a Kaplan-Meier counting process to these field data to estimate the male survival function, S(t), where we measured age, t, in years (Therneau and Grambsch 2000). We

left-truncated survival data for adults alive at the start of the analysis period, whereas we right-censored survival data for adults alive at the end of the study, emigrant males of unknown fate (n = 4), males poached (n = 2), and males translocated to other populations (n = 10). Natural immigrants (n = 3) entered the analysis at the age at first arrival and males (n = 8) translocated from other populations entered the analysis 1 year after their release to limit the influence of any adverse effects from transport or capture. We counted 6 males in extremely poor condition culled for veterinary necropsy as natural mortalities during the appropriate age interval. Finally, as in Hogg et al. (2006) and to control for effects of historical inbreeding (Hogg et al. 2006, Miller et al. 2012), we modeled age-specific male survival as a function of 2 measures of outbreeding (the source and hybridity indices; Lynch 1991) using Cox proportional hazards regression and the Efron approximation for estimating (partial) likelihoods in the Cox model (Therneau and Grambsch 2000). The NBR age-specific survival rates used in the simulations we report here are those predicted by the Cox model for the genetically rescued population at equilibrium with respect to individual levels of outbreeding (i.e., a population with median outbreeding indices equal to that calculated from the pedigree of the 2012 NBR population). We implemented the Kaplan-Meier and Cox model procedures using the R package survival version 2.38-1 (Therneau and Lumley 2014) running under R version 3.1.2. (R Core Team 2014). In the absence of hunting, bighorn sheep survival is independent of horn length (Bonenfant et al. 2009) and we applied these survival rates for the NBR (Table S1) to both hunted populations.

We measured horn length from tip to base along the top edge of keel. To obtain age-specific horn growth rates, we estimated the size of annual horn length increments, which are marked by annuli (Geist 1966). We estimated the annual increment length as the distance between 2 sequential annuli. We used measurements of annual increments to model horn growth instead of changes in total horn length to reduce the bias through premature death of hunted males. The sample sizes were sufficient to estimate the annual increments of males aged 4 to 8

years at Ram Mountain (Table S2), and 4 to 7 years at Sheep River (Table S3). Horn tips often break when fighting with other males. Without accounting for breakage at the horn tips, we obtained unrealistically long horns. Consequently, we reduced the mean of increments for older ages (Ram Mountain, 6–8 yr; Sheep River, 6–7 yr) by 2 cm and set the mean increment to 0 cm for males >8 years at Ram Mountain and >7 years at Sheep River (Tables S2 and S3). For those ages with zero increments, we set the standard deviation (SD) to the mean value of SDs (Ram Mountain, 4–8 yr; Sheep River, 4–7 yr; Table S2 and S3, respectively). With this setting we achieved realistic age-specific horn lengths for both populations. We assumed that differences in horn circumference for a given horn length did not affect the probability of reaching legal status or the probability of being shot. All animal-handling procedures at Ram Mountain and Sheep River were approved by the Animal Care Committee of the Université de Sherbrooke, affiliated with the Canadian Council on Animal Care (protocol MFB2009-1). Field methods at NBR were subject to annual review and approval by refuge staff (U. S. Fish and Wildlife Service [USFWS]) with additional optional oversight by the regional USFWS Wildlife Health Office (Bozeman, MT, USA).

Definition of Legal Male

We modeled 2 hunting regulations: 4/5 curl and full-curl (Fig. S1). Males that fulfill the regulation are called legal and can be harvested. These regulations are in general respected because, if harvested horns are >1 cm short, the trophy will be taken away and the hunter will usually be prosecuted. There are no data on males shot and left to avoid charges, but although this type of poaching may increase the mortality of sub-legal males, it will not affect the conclusions drawn from the model on how changes in hunting regulations and harvest rates affect age-structure and horn size distribution.

The probability that a male with a given horn length is legal under the 4/5 curl fits a logistic function (intercept = −19, slope = 0.25; Festa-Bianchet et al. 2014). With this probability

function, males have a 50% probability of being legal at a horn length of about 75 cm. We modeled the full-curl regulation by shifting the probability function 10 cm to the right: horns must be 10 cm longer to classify a 4/5-legal male as legal under the full-curl regulation. The Draft Management Plan for Bighorn Sheep in Alberta (2015) reported that mean horn length of harvested males increased by 7.1 cm when regulation changed from 4/5 curl to full-curl. We chose 10 cm to cover a wider range of hunting regulations ranging from a liberal (4/5 curl) to a restrictive definition (full-curl) of legal ram. The probability function of the full-curl regulation gives a male a 50% probability of being legal at a horn length of about 85 cm.

The Model

We implemented an individual-based model in the JAVA® programming language and compiled it with the javac-compiler, version 1.6.0_24 (source code available at http://github.com/s-schindler/AgeAtHarvest). In our model, males are recruited to the population at age 4 and live for at most another 11 years; therefore, they are aged from 4 to 15 years. In addition to age, a male has 2 properties: horn length (without loss of generality we focus on 1 horn only), and legal status. One time step corresponded to 1 year and at each time step a cohort of 4-year-old males recruited to the population. We drew the number of recruits and their horn length randomly from a Gaussian distribution (Table S4). Males survived according to the estimated age-specific survival rates (Table S1). Age of surviving males increased by 1 year and their horns grew by age-specific increments randomly drawn from a Gaussian distribution (Tables S2 and S3).

After 12 initial time steps, all age classes were potentially present in the population and hunting commenced. We modeled harvest rates on legal males from 0% (no hunting) to 100% (all legal males were shot), in steps of 10%. For comparison, the estimated hunting pressure on legal males at Ram Mountain is 37.5% (Pelletier et al., 2012). By definition, sub-legal males cannot be shot and therefore we did not include them in the simulation of harvest rates.

The annual biological cycle in the 2 hunted populations was as follows. Males recruited to

the population in May. Hunting season was from the end of August to the end of October and most natural deaths occurred during winter. The sequence of events in the model mirrored biological events: males entered the simulation with the randomly assigned horn lengths of 4-year-olds (Table S4). Male recruitment (May) was followed by updating the legal status of males (Jun) after which males were subjected to hunting (Aug–Oct). Following the hunting season, males were subjected to natural mortality (Nov–Mar), the age of survivors increased by 1 year, and horn size increased by annual increments (May–Aug).

We simulated population dynamics for each harvest rate (0–100%) for 100 time steps for slow and fast age-specific horn growth rates, and 2 hunting regulations (4/5 curl and full-curl). We simulated each combination of harvest rate, horn growth rate, and hunting regulation 10,000 times, each time with a different seed for the random generator. To exclude autocorrelations within simulations and to remove bias from stochasticity, we averaged the age-specific horn length and age distribution over all 10,000 replicates at specific time points. We averaged horn and age distribution over the replicates in the first year of hunting, the first 19 time steps after hunting commenced (to monitor the transition period) and at the 99th time step to calculate measures after the population reached equilibrium. Because the results during the transition did not differ from those at equilibrium, we report the latter only.

To quantify the joint dynamics of hunting regulations, harvest rates, and horn growth rates, we monitored the number, age, and horn length of males alive before and after the hunt. We also monitored the number, age, and horn length of legal males and of those harvested. For harvested males, we monitored the number of years spent as legal males before they were shot.

RESULTS

Because we performed 10,000 simulations/harvest intensity, the statistical power of our estimates is large, even when effect sizes are small. For this reason, we report the variability in the simulation data, measured by their SD, rather than confidence intervals.

Following the start of hunting of a previously unhunted population, average age at harvest initially declined but stabilized within 3–6 years (Fig. S2a). Similarly, the number of males and the number of harvested males stabilized within a few years (Fig. S2b,c). As expected, average age at harvest declined with increasing hunting pressure (Fig. 1). In populations with fast horn growth, age at harvest was consistently lower and declined more rapidly with increasing harvest rate (Fig. 1). For example, under the 4/5 curl regulation, the age at harvest in a population with fast horn growth dropped by 1.8 years, from 6.4 to 4.6 years as harvest rate increased from 10% to 100%, but it dropped by only 1.4 years, from 7.2 to 5.8 years in the population with slow growing horns. The smaller drop in age-at-harvest in populations with slow vs. fast horn growth is due to the smaller impact that changing the harvest rate has on the age distribution of harvested males in populations with slow horn growth (Fig. S3a,b). The proportion of harvested males aged 4–5 years naturally increases under increased harvest pressure, whether horns grow rapidly or slowly, but this proportion increases faster in populations with rapid than with slow horn growth rate (Fig. S3a,b).

A few years after the onset of hunting, the average horn length stabilized among harvested and surviving males. The effects of hunting on age distribution of surviving males were stronger in the population with faster horn growth (Fig. 2, Fig. S4a,b). For example, the proportion of 4-year-olds among living males nearly doubled from no hunting to 100% hunting intensity in populations with slow horn growth (Fig. S4a), but it tripled in populations with fast-growing horns (Fig. S4b). The proportion of males aged 4 or 5 years increased from 40% to 70% with slow horn growth, and from 40% to 94% with fast horn growth (Fig. S4a,b).

As hunting intensity increased from 10% to 40%, mean horn length at the population level decreased the most for males aged ≥7, especially in populations with slow horn growth (Fig. 4a). When hunting intensity exceeded 50%, <20% of surviving males were aged ≥7 (Fig. S4a), and they accounted for only 6–17% of legal males. As the harvest rate increased past 40%, the

harvest removed a greater proportion of males in the year they became legal, so that the number of harvested males did not increase by much (Fig. S5a,b).

Switching from 4/5 curl to full-curl shifted the mode of age distribution of harvested males by about 1 year, from 6 to 7 years for slow horn growth at 10–60% harvest rate (Fig. S3a,c), and from 5 to 6 years for rapid horn growth at 10–30% harvest rate (Fig. S3b,d). Regardless of horn growth rate, the harvest included fewer males aged 4–5 years and more males aged ≥7 years under full-curl than 4/5 curl regulations. Life expectancy was less affected by regulation (4/5 curl or full-curl) in populations with fast growing horns (Fig. S6). With slow horn growth, 80% of males that had survived to age 4 became legal under 4/5 curl and 57% under full curl, the rest died of natural causes without attaining legal horn status. In a population with fast horn growth, 95% reached legality under 4/5 curl and 88% under full-curl. The decrease in the number of harvested males when switching from 4/5 to full-curl was greater in populations with slow-growing horns because more males died of natural causes without becoming legal (Fig. 4). In populations with fast growing horns, however, ≥30% of males that survived to age 4 died through hunting even when hunting pressure was only 10%, regardless of the curl regulation (Fig. 4). Age-specific horn length declined with harvest pressure under both 4/5 curl and full-curl (Fig. 3 and Fig. S7).

DISCUSSION

The most important result of our simulations is that the effects of trophy hunting regulations are strongly dependent on horn growth rate. That is because as horn growth rate increases, more males become legal at a younger age, and more survive to reach the definition of legal male, regardless of whether it is set to 4/5 curl or full-curl. Therefore, harvest rates >30–40% have a more drastic effect on the age and horn size of legal males in populations with rapid horn growth rate. In these populations, many males become legal at 4–5 years of age, well before their maximum potential horn size. If harvests exceed about 30% of legal males, then <20% of adults

will reach ≥7 years and hunters would most likely encounter young legal males. Our model predicts that in populations with slow-growing horns, a switch from 4/5 curl to full-curl regulations would reduce the number of harvested males by 10–25% depending on harvest pressure, because males would become legal at older ages, when natural mortality increases (Loison et al. 1999). More males would die of natural causes before reaching legal status, compared to populations with rapid horn growth rate, where our model predicts a decline in harvest of only 2–8%.

Our simulations revealed that as harvest rates increase past 40–50%, the number of males harvested increases very little; at these very high levels of harvest most males are taken the year they become legal, and there are very few males >7 years. High harvest rates also increase the selective effects of trophy hunting; older age classes would be made up mostly of small-horned males that are illegal to harvest (Bonenfant et al. 2009). At Ram Mountain, harvest rate was approximately 37.5% (Pelletier et al. 2012). At this level of harvest, our simulation predicts a median age of harvested males of 5 years and the average life expectancy of a legal male is about 10 months; most legal males are taken the year they become legal or the following year. That compares favorably with the results from Ram Mountain, where between 1975 and 1996, 92 males that attained legal status survived on average 0.86 years after their first hunting season as legal males (SD = 1.29, range = 0–6 yr; 80% survived 0 or 1 yr). The median age at harvest was 6 years ($\bar{x}$ = 6.1 yr), but 40% were shot at 4 or 5 years of age.

As harvest rates increase, the average horn size of males decreases in the total population and among those harvested. That decline is caused by 2 factors: when harvest rates are high, males are shot at a younger age and males of any age tend to be shot as soon as their horns meet the legal definition.

A clear prediction of our model is that the average age at harvest should decrease as harvest intensity increases. Although this result appears intuitive, some empirical studies report

the opposite pattern, with age-at-harvest increasing with higher hunting pressure (Table 1). In the simulations, age-at-harvest stabilized after only 7–8 years of hunting. In all simulations, hunting initially led to a rapid decline in the average age of harvested males because unhunted populations include several legal males in many age classes, but as those are harvested, the population quickly reaches an equilibrium where most legal males are those that just became legal that year or the year before. The younger but stable age distribution predicted by our model does not match several recent observations of trophy-hunted ungulates, where the average age at harvest increased over time, particularly because of a diminishing proportion of young males (Garel et al. 2007, Festa-Bianchet et al. 2014). The increase in age of harvested males reported by recent studies may therefore suggest a decrease in horn growth rate (Garel et al. 2007, Hengeveld and Festa-Bianchet 2011, Festa-Bianchet et al. 2014, Pelletier et al. 2014), consistent with a possible evolutionary effect of selective hunting (Coltman et al. 2003, Festa-Bianchet et al. 2014, Gabriel et al. 2016, Pigeon et al. 2016).

Our model is based on data on natural survival of bighorn males from the NBR population, the only available source of this detailed age-specific information. Survival of males aged 4–8 at the NBR (Table S1) is very similar to the age-specific natural survival (excluding hunting mortality) of adult males in 2 hunted populations in Alberta (Loison et al. 1999). For example, natural survival from 4 to 9 years of age would be 0.37, 0.38, and 0.39 at NBR, Ram Mountain, and Sheep River, respectively, all populations with long-term data on age-specific survival. The precision of our estimates of survival of males >9 years is limited by the small sample size, but in most hunted populations very few males survive to that age (Festa-Bianchet et al. 2014). In very lightly hunted populations, a higher survival of older males would clearly increase the availability of trophies compared to our model's predictions.

Our simulations are relevant for other trophy-hunted species where harvest regulations are based on horn size or shape, such as other wild sheep, including Stone's (*O. dalli*; Douhard et al.

2016), and wild goats such as ibex (*Capra ibex*; Büntgen et al. 2014). For other bovids that reach near-asymptotic horn size by 2–3 years of age, such as mountain goat (*Oreamnos americanus*) or pronghorn (*Antilocapra americana*; Festa-Bianchet 2012), we expect a much weaker interplay between horn size and age. For cervids, hunting regulations are often based on number of tines rather than on antler size or shape (Strickland et al. 2001) and the relationship between number of tines and age often reaches an asymptote at 3–6 years of age, depending on the species (Mysterud et al. 2005). In those species, regulations imposing hunter selectivity and changes in harvest rate may affect antler branching pattern more than antler size, and considerable attention has been devoted, for example, to how restrictions on tine numbers may affect the harvest of young male white-tailed deer (*Odocoileus virginianus*; Strickland et al. 2001).

MANAGEMENT IMPLICATIONS

Our simulations provide managers with guidelines to the possible consequences of varying harvest rates in bighorn sheep populations with different horn growth characteristics. Our model suggests that harvest rates above 30–40% of legal males will lead to a marginal increase in the harvest while reducing the average horn size and shifting the age distribution of males towards those aged 4–6 years. The determination of harvest rates of legal males, however, remains a major challenge. Our simulations imply that a young age structure indicates a high harvest rate, especially under the slow versus fast growth scenario. Accurate measurements of the first 4 growth increments would allow managers to estimate population-specific horn growth rates at ages before males become vulnerable to hunting. This information can be used to assess the likely impacts of different hunting regulations, limit the effect of trophy hunting on male age structure, reduce the risk of artificial selection, and increase the average age and horn size of harvested males. The optimal regulation will differ between herds of different horn growth rates. A combination of full-curl definition of legal male and quotas may be required in populations with rapid horn growth. In populations with slow horn growth, a full-curl regulation may reduce

the harvest sufficiently without the imposition of quotas.

ACKNOWLEDGMENTS

We thank S. Cubaynes, B. Kendall, I. Booksmythe, and A. Tilquin for assistance with stochastic analyses, A. Grüning for advice on Java, and E. Vander Wal for help with the literature. We thank J. A. Deere and E. G. Simmonds for constructive comments on our manuscript. We acknowledge the use of computing facilities of the University of Oxford Advanced Research Computing and the S3IT at the University of Zurich. S.S. has been funded by an Advanced ERC grant (LEED) awarded to T. Coulson while conducting some part of this research. Research on bighorn sheep at Ram Mountain and Sheep River was supported by the Natural Sciences and Engineering Research Council of Canada, Alberta Fish and Wildlife, and the Alberta Conservation Association. Research by J. Hogg at the NBR was supported by The Charles Engelhard Foundation, The Eppley Foundation for Research, and The National Geographic Society.

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Associate Editor: Kelly Proffitt.

FIGURE CAPTIONS

Figure 1 Age at death [yr] of harvested bighorn males under varying hunting pressure [% harvested] and 4/5 curl regulation for slow-growing (circles) and fast-growing (squares) horns. Error bars indicate standard deviations.

Figure 2 Age distribution of harvested bighorn males under high hunting pressure (solid lines, 40% harvested) and low hunting pressure (dashed lines, 10% harvested) when horns grow slowly (black lines) or grow fast (red lines). Hunting is modeled according to the 4/5 curl regulation.

Figure 3 Age-specific [yr] horn length [cm] of all bighorn males at the start of the hunting season for low hunting pressure (10% harvested, circles) and high hunting pressure (40% harvested, squares) under the 4/5 curl regulation for populations with A) slow growth or B) fast growth. If hunting pressure is high in the population with fast-growing horns, no male survives until age 15. Error bars indicate standard deviation.

Figure 4 Fraction of a cohort of bighorn males that survived to 4 years of age and died of natural causes for varying hunting pressures [% harvested] and hunting regulations (4/5 curl = empty symbols, full-curl = filled symbols). Circles refer to slow horn growth, squares to fast horn growth.

Table 1. Empirical studies assessing the effects of hunting on demography, trophy measures, and life-history of ungulates and carnivores.

Species	Traits studied	Trait trends	Methods	Reference
Ungulates and carnivores	M age	Reduction of mean M age.	Population census.	Milner et al. 2007
Mouflon (*Ovis gmelini musimon*)	Age and horn size	Age of desirable trophies increased by ~4 yrs. Proportion of young M in the harvest decreased. Horn size decreased under harvesting.	Compared harvested M of populations under hunting with a protected population.	Garel et al. 2007
Thinhorn *(Ovis dalli*)	M age	M with rapid horn growth are shot earlier in life than slow-growers.	Horn size of harvested M.	Loehr et al. 2010
Bighorn	Horn length and circumference	Lower decrease in length for harvested M (−11%) than	Compared horn trends between shot M and all M.	Pelletier et al. 2012

		overall (−20%). Decline in circumference not different.		
Bighorn	Horn length, age, counts	No. harvested M and horn size decreased. Age-at-harvest increased.	Size measurements on harvested M.	Festa-Bianchet et al. 2014
Red deer (*Cervus elaphus*)	Antler size	No consistent temporal pattern.	Measurements of harvested M and entries in trophy shows.	Rivrud et al. 2013
Impala (*Aepyceros melampus*)	Horn length and age-at-harvest	Horn length decreased (−4%) and age-at-harvest decreased.	Size of harvested trophies.	Crosmary et al. 2013
Greater kudu (*Tragelaphus strepsiceros*)	Horn length and age-at-harvest	Horn length increased (14%) and age-at-harvest increased, possibly because of decreasing harvest pressure.	Size of harvested trophies.	Crosmary et al. 2013

Schindler et al.

Sable antelope (*Hippotragus niger*)	Horn length and age-at-harvest	Horn length decreased (−6%), no change in age-at-harvest.	Size of harvested trophies.	Crosmary et al. 2013
Trophy ungulates	Trophy size	Decline in trophy size for most species.	Record book entries.	Monteith et al. 2013
Brown bear (*Ursus arctos*)	Age structure and body mass	Ratio of yearlings to adult F and yearling body mass declined over time. Mass of shot F showed no trend, whereas mass of monitored F decreased.	Compared data from monitoring project with hunting records.	Leclerc et al. 2016

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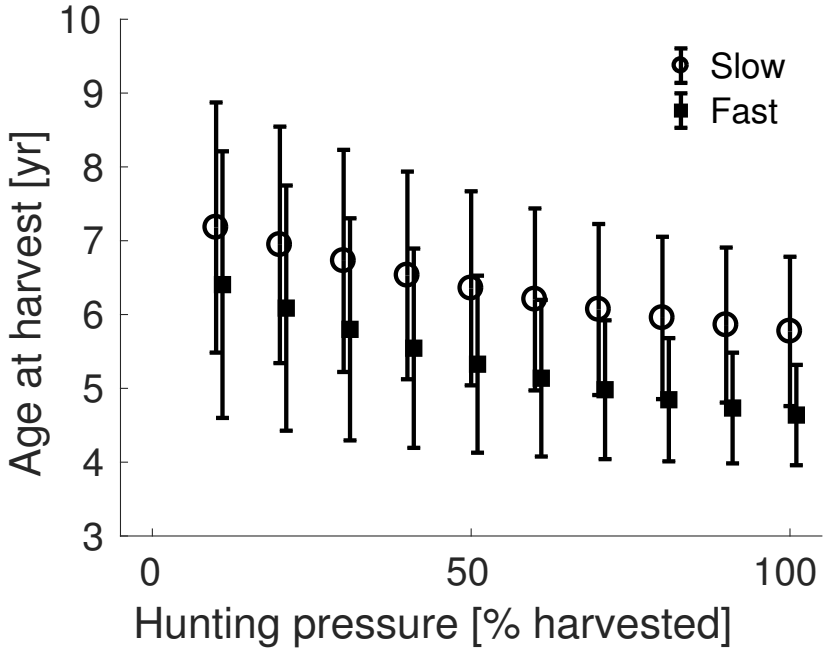
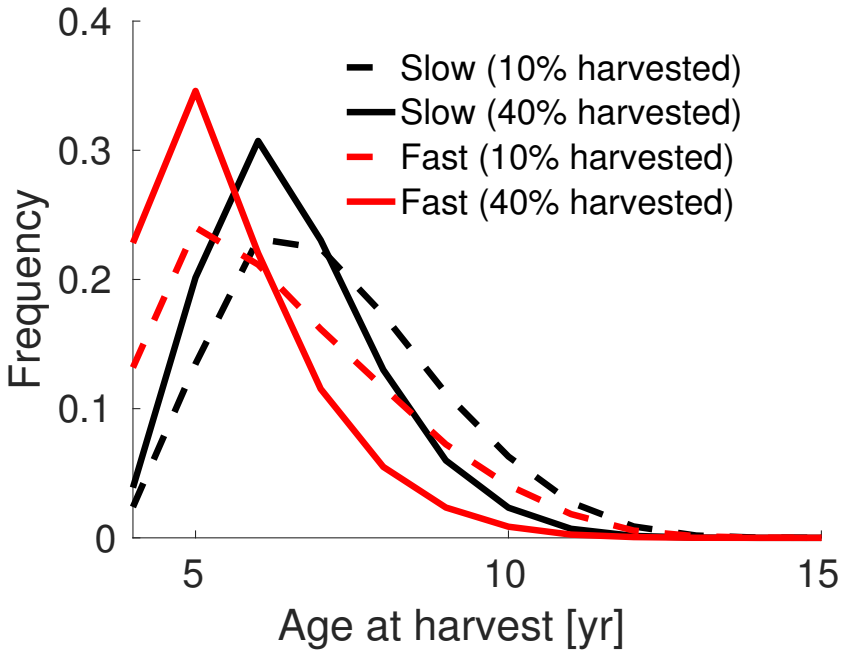
Article Summary: We show that the effect of hunting regulations on age structure and trophy size depends strongly on the rate of trophy growth, which naturally varies between populations of the same species. This implies that the optimal hunting regulation differs between herds of different trophy growth rates.

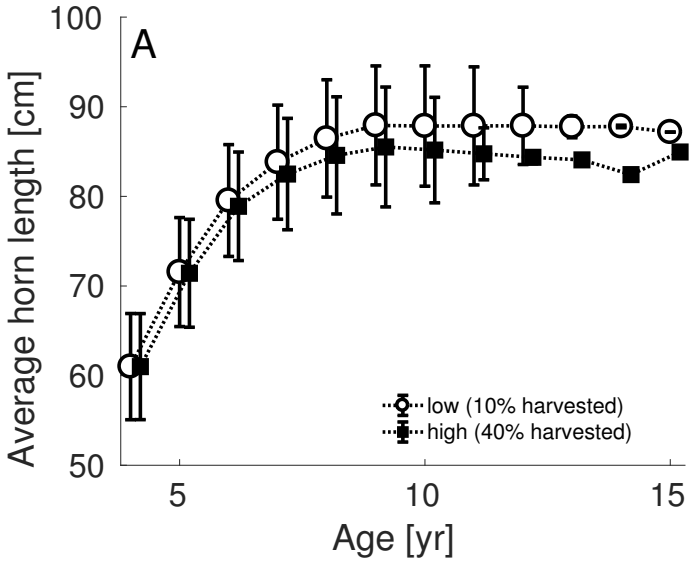
Figures for

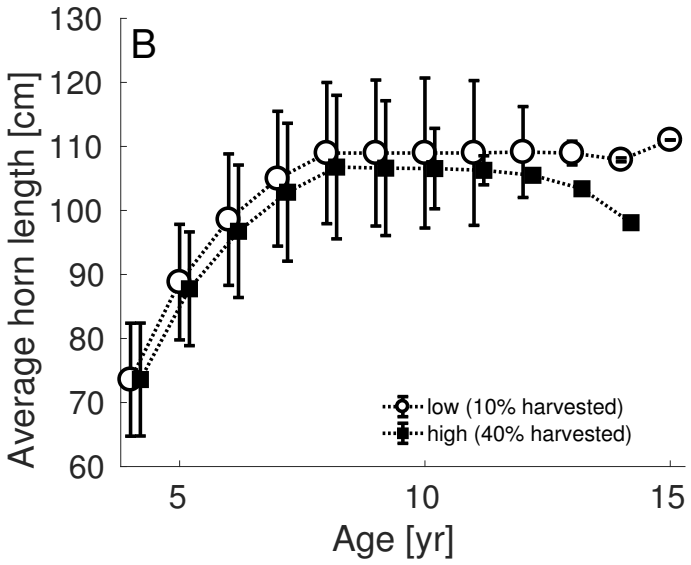
Hunting effects on age-structure and horn size distribution in bighorn sheep.

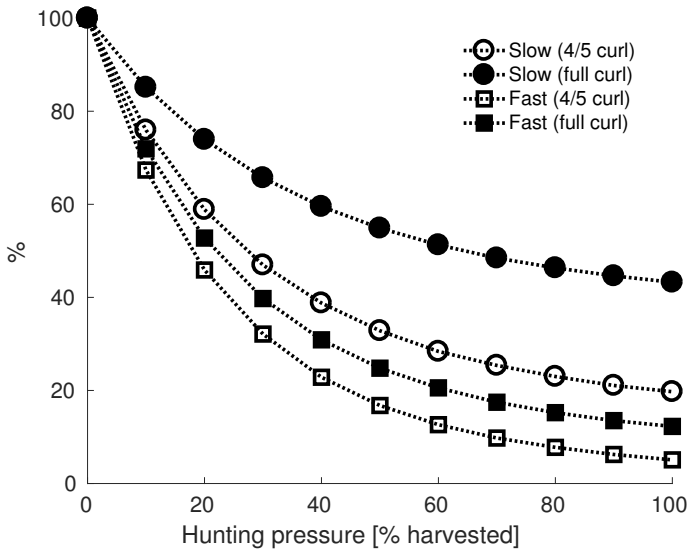
Susanne Schindler, Marco Festa-Bianchet, John T. Hogg & Fanie Pelletier

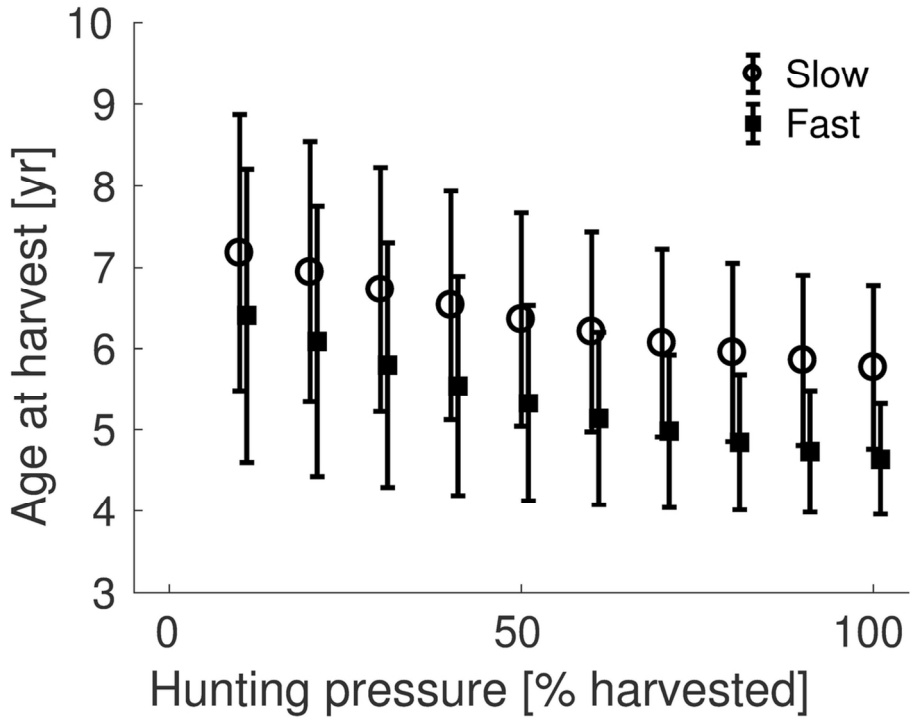



0.4
0.3
0.2
0.1
0
Frequency
5
10
15
Age at harvest [yr]
Slow (10% harvested)
Slow (40% harvested)
Fast (10% harvested)
Fast (40% harvested)


A
Average horn length [cm]
100
90
80
70
60
50
5
10
15
Age [yr]
low (10% harvested)
high (40% harvested)


B
Average horn length [cm]
130
120
110
100
90
80
70
60
5
10
15
Age [yr]
low (10% harvested)
high (40% harvested)


100
80
60
40
20
0
%
0
20
40
60
80
100
Hunting pressure [% harvested]
Slow (4/5 curl)
Slow (full curl)
Fast (4/5 curl)
Fast (full curl)



Fraction of a cohort of bighorn males that survived to 4 years of age and died of natural causes for varying hunting pressures [% harvested] and hunting regulations (4/5 curl = empty symbols, full-curl = filled symbols). Circles refer to slow horn growth, squares to fast horn growth.

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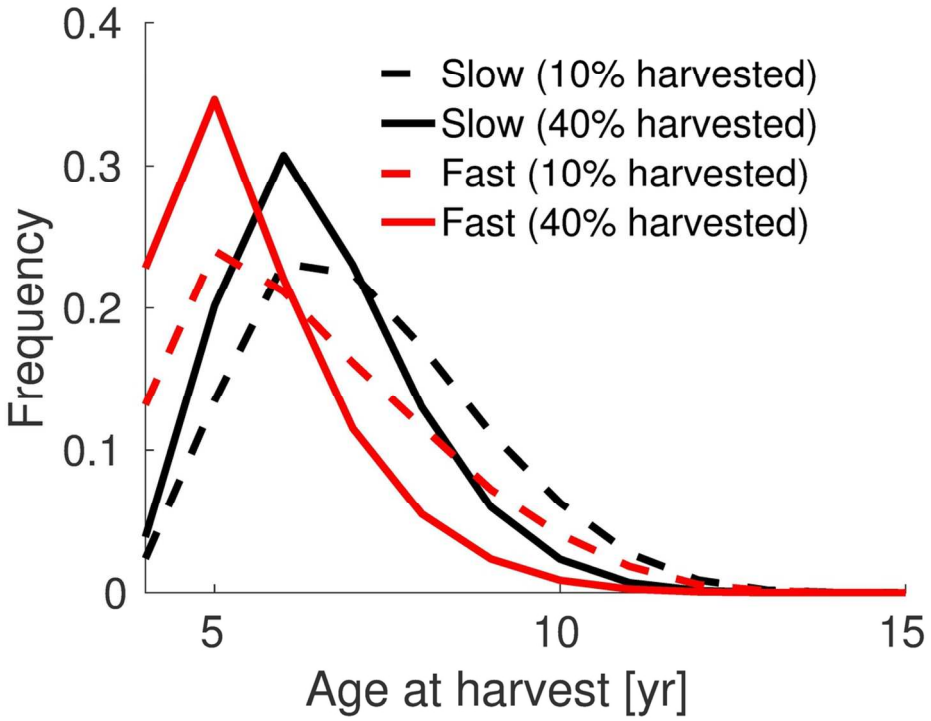

Age distribution of harvested bighorn males under high hunting pressure (solid lines, 40% harvested) and low hunting pressure (dashed lines, 10% harvested) when horns grow slowly (black lines) or grow fast (red lines). Hunting is modeled according to the 4/5 curl regulation.

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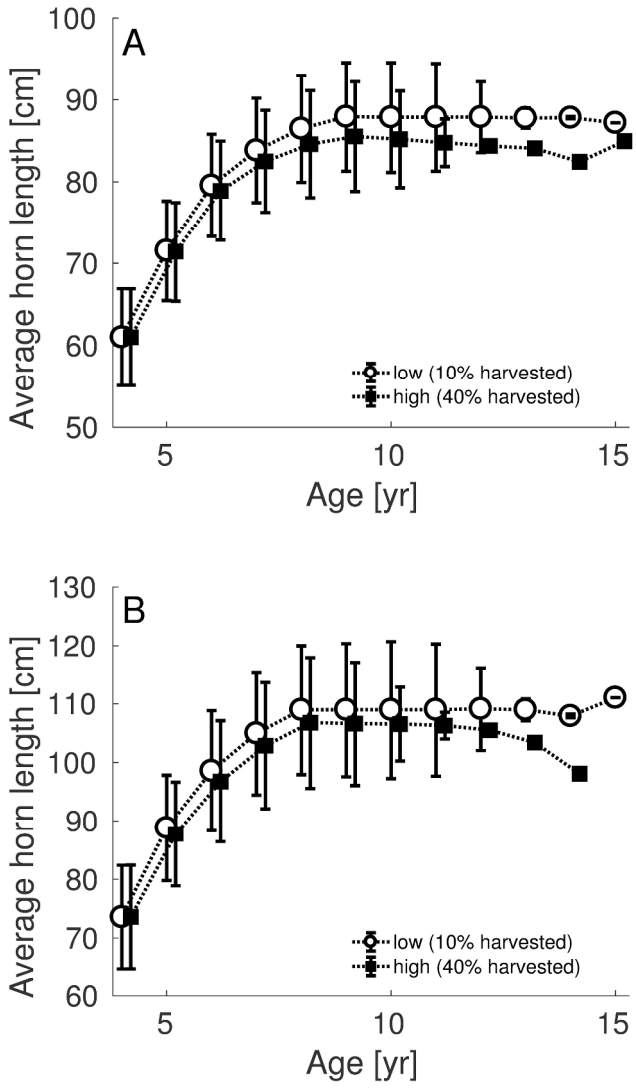

Age-specific [yr] horn length [cm] of all bighorn males at the start of the hunting season for low hunting pressure (10% harvested, circles) and high hunting pressure (40% harvested, squares) under the 4/5 curl regulation for populations with A) slow growth or B) fast growth. If hunting pressure is high in the population with fast-growing horns, no male survives until age 15. Error bars indicate standard deviation.

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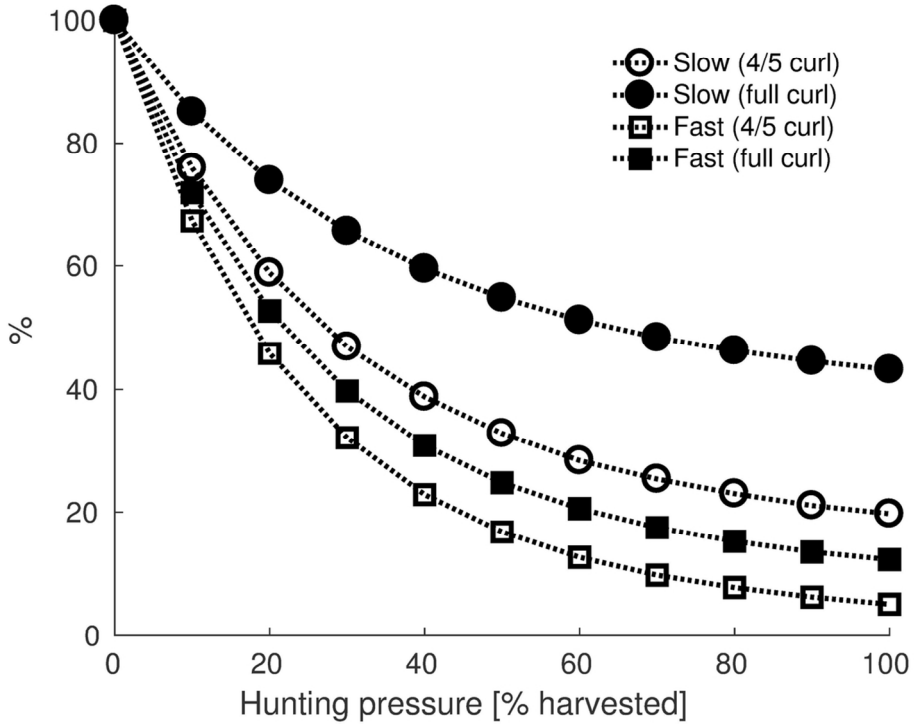

Fraction of a cohort of bighorn males that survived to 4 years of age and died of natural causes for varying hunting pressures [% harvested] and hunting regulations (4/5 curl = empty symbols, full-curl = filled symbols). Circles refer to slow horn growth, squares to fast horn growth.

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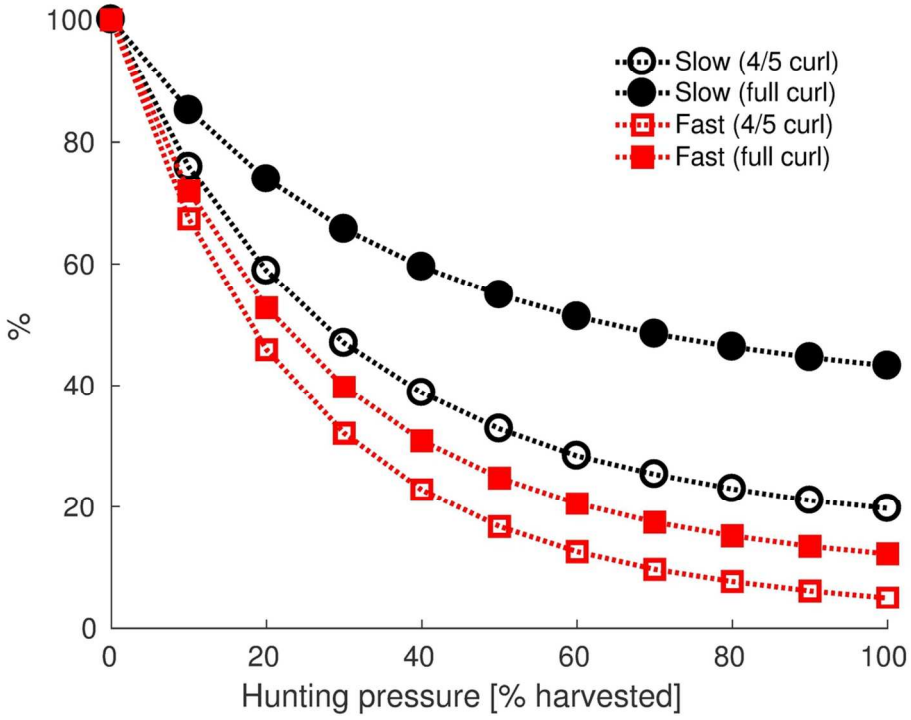

Online color version of fig 4

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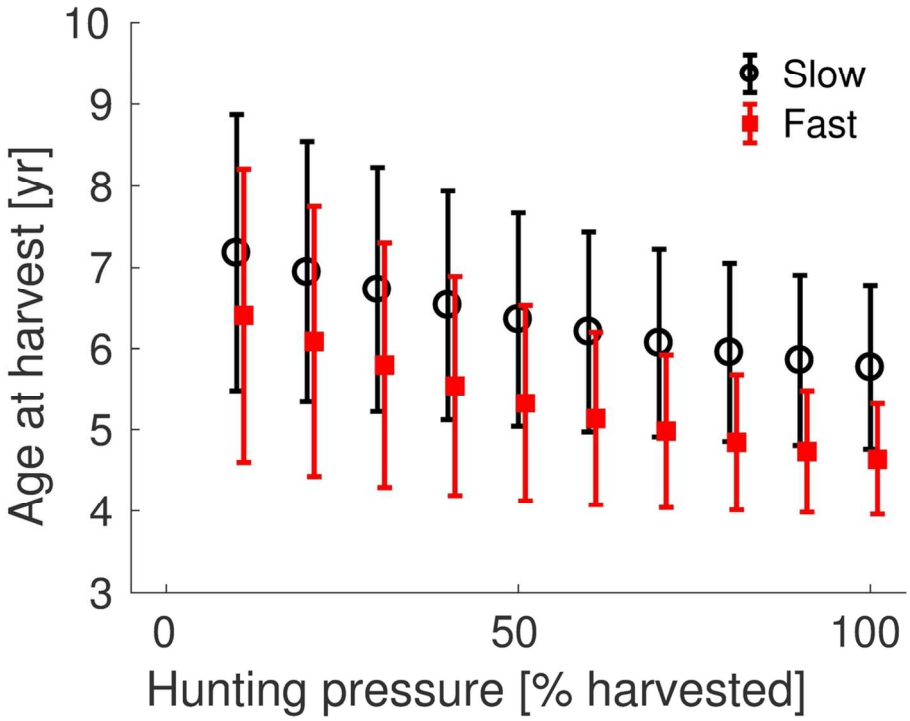

Online color version of fig 1

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